Journal of Experimental Marine Biology and Ecology 501 (2018) 83–89

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Metabolic responses to temperature in a sedentary reef fish, the bluebanded goby (*Lythrypnus dalli*, Gilbert)

Racine E. Rangel*, Darren W. Johnson

Department of Biological Sciences, California State University Long Beach, 1250 Bellflower Blvd, Long Beach, CA 90840, USA

ARTICLE INFO

Keywords:
Bioenergetics
Climate change
Metabolism
Oxygen consumption
Thermal sensitivity
Trade-offs

ABSTRACT

As climate continues to change, many marine species will experience both an increase in average temperature and more extreme diel and seasonal fluctuations. Understanding how these variations in ocean temperature affect processes such as metabolism and energy consumption is important for many species, and may be particularly important for sedentary species that cannot make large-scale movements in response to changes in environmental conditions. We examined how metabolic rates and energetic demands responded to temperature in a temperate reef fish, the bluebanded goby (*Lythrypnus dalli*). Using respirometry, we estimated resting oxygen consumption (VO_2) for 42 *L. dalli* individuals of varying sizes and calculated metabolic rates (*MR*) at three different temperatures (13 °C, 16 °C, and 20 °C). As predicted, VO_2 and *MR* increased significantly with temperature and mass, but the rate of temperature-dependent increase in metabolism indicated a very high degree of thermal sensitivity for *L. dalli* (Q_{10} value for VO_2 was 5.21 across the range of experimental temperatures). The mass-scaling exponent (b) was estimated to be 0.95 and aligned closely with other benthic species. Our results suggest that changes in temperature – especially those that occur over weeks and seasons – likely play a significant role in the ecology of these gobies. Long-term increases in seawater temperature will either necessitate an increase in foraging and consumption, or drive costly trade-offs between metabolism and processes such as growth and reproduction.

1. Introduction

In aquatic environments, temperature is a constantly changing factor that can significantly alter the metabolism, growth, and reproduction of many organisms (Killen et al., 2016; Kordas and Harley, 2016; Petes et al., 2007). Water temperature varies on many timescales (e.g., seasonal warming and cooling patterns, diel changes associated with solar heating and tidal mixing), and temperature fluctuations may play an important role in the functional ecology of species (Crozier and Hutchings, 2014; Edwards and Richardson, 2004; Harley et al., 2006). In addition, there is a growing concern about climate change and long-term increases in water temperature. Current climatic models project an overall increase in average ocean temperatures by the end of the century (Stocker et al., 2013). As climatic conditions continue to change, it is expected that temperatures will not only become warmer but also more variable (e.g., greater duration, size, and frequency of El Nino/Southern Oscillation events; Reaser et al., 2000; Walther et al., 2002). However, many species of aquatic organisms may already be living near or at their thermal tolerance threshold, and may have limited capacity to acclimate to further temperature increase (Eliason et al., 2011; Stillman, 2003; Tewksbury et al., 2008). Increases in temperature beyond these limits may result in failure of physiological systems, reduction of reproductive success, and elevated mortality rates (Hoegh-Guldberg and Bruno, 2010; Somero, 2002; Stocker et al., 2013).

Sedentary species that have little capacity for large-scale movement typically do not redistribute themselves in response to changes in their environment. For these species, short-term fluctuations in water temperature may be ecologically important, and long-term increases in temperature may be especially concerning. It has been well established that fish metabolism is directly related to environmental temperature (Angilletta et al., 2002; Fry, 1971; Gillooly et al., 2001). Higher temperatures may accelerate physiological rates and result in higher demands for energy (Dillon et al., 2010; Johansen et al., 2015). In turn, these energetic demands may have direct effects on feeding rate, growth, and/or reproduction. A necessary first step toward understanding the effects of temperature on a population is to conduct controlled studies of thermal sensitivity. One measure of thermal sensitivity is Q_{10}, the factor by which a rate changes over a 10 °C change in temperature (Schmidt-Nielsen, 1997). It has been suggested that teleost fish have an average Q_{10} value of approximately 2.5 (Brett and Groves,

* Corresponding author.
E-mail addresses: racine.rangel@student.csulb.edu (R.E. Rangel), darren.johnson@csulb.edu (D.W. Johnson).

https://doi.org/10.1016/j.jembe.2018.01.011
Received 14 September 2017; Received in revised form 24 January 2018; Accepted 28 January 2018
Available online 03 February 2018
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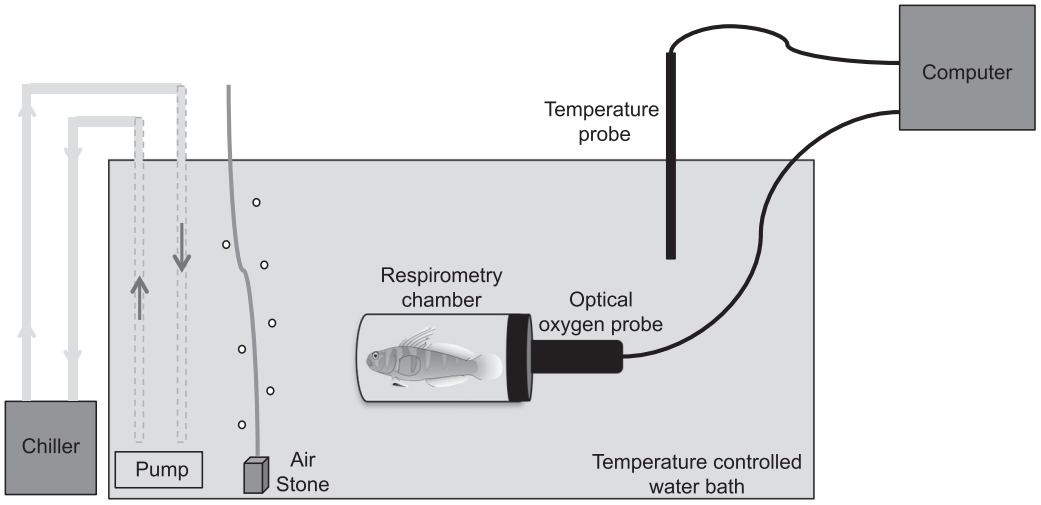

Fig. 1. Schematic representation of static respirometry system used to measure resting metabolic rate of bluebanded gobies (*Lythrypnus dalli*). Arrows indicate the direction of water flow.

1979); however, Q_{10} values may vary substantially among ectothermic species and populations (Angilletta et al., 2002; Somero, 2002). Thermal sensitivity may be influenced by several factors including body size (Clarke and Johnston, 1999; Di Santo and Lobel, 2016), lifestyle (Killen et al., 2010), phylogeny (Clarke and Johnston, 1999) and local adaptation to thermal regimes (Donelson and Munday, 2012; Pulgar et al., 2005).

We studied the bluebanded goby (*Lythrypnus dalli*), a temperate reef fish that exhibits very limited large-scale movement (home ranges are $< 0.5\,m^2$), and is a species that may be representative of other, small-bodied fishes that live on temperate reefs. *L. dalli* is a small (adult standard length 18–45 mm) simultaneous hermaphrodite and their reproductive success is largely based on their size and position within a dominant social hierarchy in which larger individuals function as males (Rodgers et al., 2005; Wiley, 1976). *L. dalli* is found from Central California to the Gulf of California, Mexico and inhabits subtidal reefs from 3 to 76 m in depth, (Wiley, 1976). Individuals of *L. dalli* tend to spend their lives on the reefs to which they settled (St. Mary, 1993; St. Mary, 1994; Wiley, 1976). They forage regularly and frequently within their home ranges, and their main diet is composed of planktonic copepods (Behrents, 1983; Hartney, 1989). At our study location, average monthly temperatures range between 14 °C to 21 °C (Padilla-Gamino and Carpenter, 2007). It has been observed that breathing of *L. dalli* becomes erratic at temperatures of 23 °C and higher (Love, 2011), but no measurements of metabolic rates have been published for this species at any specific temperature. The goals of this study were to (1) characterize how temperature and body mass affect resting metabolic rate of *L. dalli* and (2) evaluate how sensitive *L. dalli* is to temperature change by calculating a Q_{10} coefficient for metabolism of this species.

2. Methods

2.1. Fish collection and acclimation

Divers collected *L. dalli* specimens from Santa Catalina Island, California, USA in May 2015. Temperature at time of collections was between 17 °C and 18 °C. Per institutional requirements, fish were quarantined for a 24-h period as a precaution to identify any sick individuals and minimize the potential spread of pathogens. All gobies appeared healthy, and after this period fish were housed at the California State University Long Beach Marine Laboratory. Gobies were placed in tanks that were plumbed into a 3700-liter re-circulating seawater system. This system was periodically flushed with fresh seawater, and tanks were exposed to a 12-h light:12-h dark photoperiod. All fish were held at 16 °C, and a salinity of 34 ppt for three months before the start of experiments to minimize any effects from varying environmental history between individuals. At each of our target temperatures (13 °C, 16 °C, and 20 °C), fish were housed in multiple tanks (3, 5, and 5 tanks per temperature treatment), and these tanks were interspersed throughout the marine lab. Water quality (including temperature, ammonia, nitrite, nitrate, and pH) was measured daily in the experimental tanks, and nitrogenous waste was low throughout the study. *L. dalli* specimens were measured to obtain standard length (SL) and photographed for identification after collection. Within the study population, vertical banding patterns were noticeably different among individuals, and individual fish were identified by a combination of tank, body size, and banding pattern. Fish were fed frozen mixtures of mysis shrimp and brine shrimp from San Francisco Bay Brand ad libitum one to two times a day. Each fish in our study was tested at a single temperature only.

To minimize the effects of short-term metabolic compensation, changes to subsequent temperature treatments occurred with a 1 °C change every other day until desired temperatures of 13 °C or 20 °C were reached. Individuals were then allowed to adjust for at least a week prior to testing to allow enough time for any metabolic compensation to conclude. It has been observed for many fish species that after a fish experiences an initial temperature change, there is a short-term response that may compensate for changes in temperature. Barrionuevo and Fernandes (1998) have shown that this compensation response ceases after three to four days and oxygen consumption subsequently returns to normal. After such a period individuals may be considered fully acclimated to the new temperature (Bullock, 1955; Rummer et al., 2014).

2.2. Measuring oxygen consumption in L. dalli

We measured oxygen consumption using an optical dissolved oxygen probe within a closed respirometry system (Q-box AQUA, Qubit systems, Canada). Prior to the start of each trial, individuals were weighed (g), displacement volumes were measured, and individuals were fasted for a 24-h period to ensure a post-absorptive state (Chabot et al., 2016). Fish were placed in a 0.049-liter acrylic chamber, which was submerged in a 95-liter water bath that was held constant at the desired water temperature. Fish were allowed to acclimate for 40–60 min before the start of the trial (Fig. 1). The experimental tank containing the respirometry chamber was covered to prevent any disturbances to the individual being tested. Trials were run until ≈80% of the starting oxygen concentration was consumed within the chamber. This typically occurred within 40 min, and three measurements of oxygen consumption over time were obtained for each fish (see best practices in Clark et al., 2013). The first of the three measurements was excluded from analysis to maintain consistency and VO_2 ($mgO_2\,h^{-1}$)

was calculated from the average of the last two measurements of O_2 consumption. After each trial, a control trial containing only seawater (a blank) was run in order to account for oxygen consumption by microbes in the seawater. A linear regression of oxygen concentration over time was used to estimate the rate of oxygen consumed by each fish in the chamber (the slope of the regression line was used to estimate consumption rate). Oxygen consumption rates (in units of $mgO_2\,h^{-1}$), were calculated using the formula:

$$VO_2 = R \times (V_{total} - V_{fish}) - (V_{total} \times Bl)$$

where R is the slope of oxygen consumption for each individual, Bl is the blank slope, and V is the adjusted volume of water in the chamber (overall volume of the acrylic chamber minus the displacement volume of each individual goby). Mass-specific oxygen consumption, MO_2 ($mgO_2\,g^{-1}\,h^{-1}$) was calculated by dividing VO_2 by the mass of the fish (g).

2.3. Effects of mass and temperature on oxygen consumption

To assess the effect of temperature change on overall oxygen consumption rates, Q_{10} values were calculated across temperature treatments. In order to estimate a Q_{10} value for VO_2, in our study we needed to account for the fact that oxygen consumption also scales with body mass. Despite initial similarities in mass among fishes in each temperature treatment, there was some mortality during the study that resulted in a slight imbalance in the study design. In particular, gobies in the 13 °C group were heavier, on average (see Results). This feature would have confounded the effects of temperature and mass, if estimated separately. In addition, variation in body mass accounted for a lot of the variation in VO_2 (see Results), and estimating the effects of mass and temperature together increased the precision of our estimates. To describe the effects of mass and temperature on VO_2, we fit the following equation to the observed measures of VO_2:

$$VO_2 = (aW^b)(Q_{10}^{T/10^\circ}) \quad (1)$$

where W is mass and T is temperature (in °C). Parameters a and b describe how VO_2 scales with body mass: b is the mass scaling exponent, and a describes dependence on body mass as mass approaches zero. Within this framework, one can test for a significant effect of mass by evaluating whether b is significantly different from 0. Similarly, one can test for an effect of temperature by evaluating whether Q_{10} is significantly different than a value of 1, since Q_{10} is a multiplier. To fit the mass-and temperature-dependent model to the data, we linearized Eq. (1) by taking the natural logarithm of both sides of the equation. After this transformation, the logarithm of VO_2 could be modeled as a linear combination of temperature and the logarithm of mass. This analysis assumes a lognormal error distribution. This is appropriate because measures of metabolism must take on positive values and because data on metabolic rates often follow a lognormal distribution (e.g., Chabot et al., 2016; Killen et al., 2017). We used a linear, mixed effects model to estimate parameter values because some fish were housed in the same tanks during the experiment. We included tank identity as a random factor in this analysis. This structure allowed us to test the effects of temperature and mass while accounting for any shared effects of fish being in the same tank. Parameters were estimated using the *lme4* package in R (Bates et al., 2014). In this analysis, the antilog of the intercept estimates a, the linear coefficient for mass estimates b, and the antilog of the temperature coefficient estimates Q_{10}. To compare the Q_{10} value for *L. dalli* to other teleost species that are benthic, small (0.19–60.0 g), and have small home ranges, we compiled a data set of Q_{10} measurements obtained from a literature search conducted using Google Scholar, and the California State University Long Beach Library OneSearch database. This yielded a sample of 33 estimates of Q_{10} values for metabolic rate from 27 species (Appendix 1).

2.4. Effects of temperature on metabolism and daily consumption rates

Oxygen consumption is directly related to energy use and metabolic rate. To illustrate the effects of temperature on metabolism, we converted VO_2 values ($mgO_2\,h^{-1}$) to metabolic rates ($cal\,g^{-1}\,h^{-1}$) by dividing a goby's VO_2 values by its mass (g) and then multiplying by the oxycalorific equivalent of 3.25 cal/mgO_2. This is considered to be the appropriate oxycalorific equivalent for respired oxygen in teleost species (Brett and Blackburn, 1978; Elliott and Davison, 1975) based on diet and composition of prey, in terms of protein, carbohydrates, and fats (Brett and Groves, 1979). Although we did not conduct any statistical analyses on metabolic rates (statistical inferences would be redundant with those made on VO_2), examining metabolic rates provided a useful way of evaluating the effects of temperature on energy consumption. In addition, with our data on temperature-dependent oxygen consumption (VO_2), we could calculate the average metabolic demand at various temperatures, and the feeding rates that would be necessary to sustain these demands. Using Eq. (1) and the associated parameter values estimated from our data, we calculated VO_2 values for a goby of average mass (0.83 g). To quantify the consequences that increasing temperature may have for feeding rates, daily consumption rates (CR) at each temperature (13, 16, and 20 °C) were calculated as follows:

$$CR = (VO_2 * 24hr * O)/P \quad (3)$$

where VO_2 is oxygen consumption ($mgO_2\,h^{-1}$), O is the oxycalorific equivalent (3.25 cal/mgO_2), and P is the caloric value of prey. *L. dalli* primarily consume planktonic copepods (Hartney, 1989) therefore, a daily maintenance ration was calculated by using the known caloric value of adult copepods, $P = 5.88 \times 10^{-3}$ cal/copepod (Theilacker and Kimball, 1984).

3. Results

3.1. Effects of temperature on L. dalli oxygen consumption

Of the 42 gobies that were collected, there were 11 tested at 13 °C, 15 at 16 °C, and 16 at 20 °C. Mean values (SD) for individual body mass for the 13 °C, 16 °C, and 20 °C treatments were 1.03 (0.53), 0.70 (0.44), and 0.75 (0.31) g, respectively. Mean values of oxygen consumption ($mgO_2\,h^{-1}$) were 0.14 (0.09 SD) at 13 °C, 0.19 (0.15) at 16 °C, and 0.34 (0.24) at 20 °C. Oxygen consumption rates (VO_2 values) increased with both weight and temperature (Fig. 2), and both of these effects were significant. The initial dependence on body mass (parameter a in Eq.

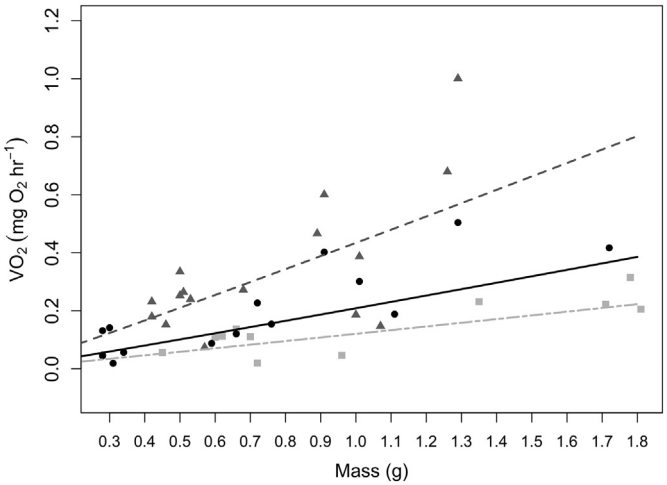

Fig. 2. Effects of body mass and temperature on oxygen consumption (VO_2). Data are presented for fish at temperatures of 13 °C (squares, dot-and-dashed line), 16 °C (circles, solid line), and 20 °C (triangles, dashed line). Lines represent predictions from a temperature and mass dependent model of oxygen consumption (see Eq. (1) in the main text).

Table 1
Mean (SE) values for metabolic rate (MR) at various temperatures and consumption rates that would be required to meet the demands for metabolic energy.

Temperature °C	MR J g^{-1} h^{-1}	Consumption rate kcal d^{-1}	Number of prey (copepods per day)
13	0.57 (0.07)	0.00111 (0.0002)	188
16	1.07 (0.14)	0.00148 (0.0003)	251
20	1.86 (0.19)	0.00266 (0.0005)	453

(1)) was estimated to be 0.015 (95% CI: 3.60×10^{-3}, 0.0615), and the mass-scaling exponent (b) was estimated to be 0.95 (95%: CI 0.59, 1.31). The Q_{10} value for VO_2 was estimated to be 5.21 (95% CI: 2.25, 12.07), suggesting that for a 10 °C increase in temperature, oxygen consumption (and derived quantities such as metabolic rate) would increase by a factor of 5.21.

3.2. Metabolic rates and prey consumption rates of L. dalli

Metabolic rate increased substantially with temperature, and across the temperature range tested, the increases in metabolic rate would result in a considerably greater demand for energy (Table 1). To meet these energetic demands at higher temperatures, gobies would need to consume many more prey. For example, at 13 °C a typical goby would need to consume 188 copepods per day, whereas the same goby would need to consume 453 copepods per day at 20 °C (Table 1).

4. Discussion

This study revealed important information about the thermal sensitivity and size scaling of metabolic rate in *L. dalli*. Regarding the relationship between mass and metabolism, we calculated that *L. dalli* has a mass-scaling exponent of 0.95. This value is higher than 3/4, which is what one would expect if metabolic rate were limited primarily by internal transport of resources and wastes (West et al., 1997). Although relatively high, the mass-scaling exponent was within the range reported for other species of teleost fishes. Clarke and Johnston (1999) have reported that teleost fishes have scaling exponents that vary widely (b = 0.43–1.26) with a mean value that was significantly greater than a 3/4 relationship (b = 0.793 SE = 0.011). For *L. dalli* our estimate of the mass scaling exponent (b = 0.95) is more closely aligned with the values reported by Killen et al. (2010) for species with similar benthic lifestyles (mean = 0.802; range of b = 0.60–1.30). The metabolic level boundaries (MLB) hypothesis explains how the value of b may be expected to vary across species based on their lifestyle and overall activity rate (Glazier, 2005, 2008; Killen et al., 2010). For example, pelagic species tend to have high sustained levels of aerobic activity as well as higher resting metabolic rates and elevated maintenance costs that are limited by surface area, which results in a lower value of b (Killen et al., 2010). Benthic species rarely undergo active pursuit of prey items and live their life around and within substrate that allows them constant access to refuge from predation. Such species are expected to use less energy for activity and their metabolic demands are often adequately met by surface-dependent processes. For these species, metabolic scaling may depend more directly on tissue mass, which could result in mass-scaling exponents that are between 0.75 and 1 (Glazier, 2005; Killen et al., 2010). Our observed value for *L. dalli* is consistent with the MLB hypothesis. Although *L. dalli* is a benthic species, it exhibits a moderate amount of activity. Gobies will regularly forage by darting short distances (< 40 cm) into the water column, but they do not engage in active and sustained pursuit of prey. Our results for *L. dalli* support the idea that low-energy benthic fishes will have metabolic scaling exponents between 0.75 and 1 (Glazier, 2005, 2006; Killen et al., 2010; Killen et al., 2016).

Regarding thermal sensitivity, our results suggest that *L. dalli* has a metabolic rate that is relatively sensitive to increases in temperature (Q_{10} = 5.21). This value falls within the range observed for other sedentary fishes, but it is on the upper end of the estimated distribution (Fig. 3). We believe one reason for the high sensitivity may be that our study population is adapted to a fairly consistent thermal regime. If the adaptations that enable thermal tolerance are costly to maintain, then these adaptations may be reduced in environments that are thermally stable (Eme and Bennett, 2010). *L. dalli* normally resides on rocky reefs deeper than 3 m. At these depths, the temperatures at Santa Catalina Island are relatively stable over time. For example, during August to October 2016, water temperature recorded at 8 m depth had diel changes between 1 and 6 °C with an average, daily range of 3.4 °C. By comparison, Eme and Bennett (2010) found that Q_{10} values for the common goby (*Bathygobius fuscus*), and an undescribed sandflat goby species (*Bathygobius* sp.) – two tropical, intertidal species that experience a much wider range of temperatures (diel changes of 6–12 °C in tidepools) – were roughly five times lower in magnitude than those for *L. dalli* (Q_{10} = 1.06–1.12 vs. 5.21). Similar relationships between Q_{10} and thermal regime have been observed for species of sculpin (Graham, 1970; Morris, 1961) and other intertidal gobies (Barlow, 1961).

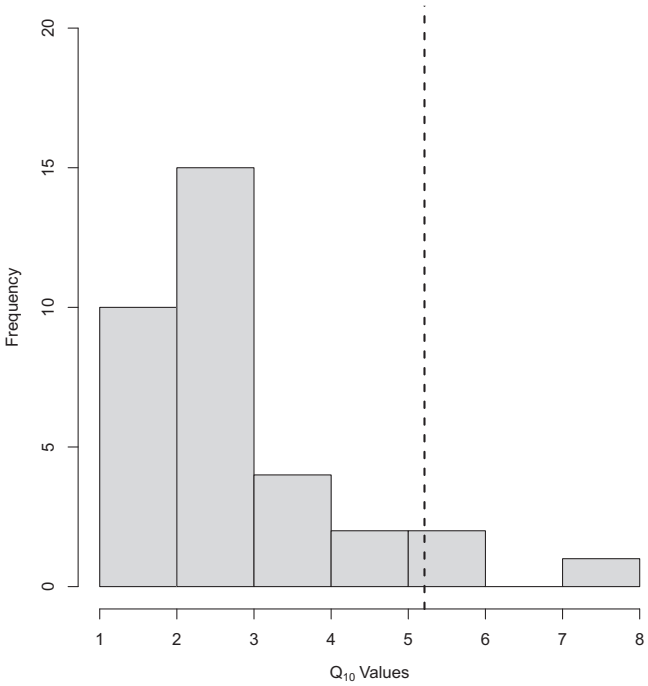

Fig. 3. Frequency distribution of published Q_{10} values for a sample of small, benthic fishes with small home ranges (n = 27 species). Dotted line represents the Q_{10} value of *L. dalli*.

It is possible that acclimation to laboratory conditions may affect Q_{10} values, but we believe such effects would be minimal in our study. Fish may lower their metabolic rates in captivity (e.g., Pérez-Casanova et al., 2008; Xie et al., 2017; Zeng et al., 2011), but for the majority of their time in the lab, fish in our study were all held under the same conditions (including temperature and feeding level). Exposure to the temperature treatments was short relative to the total time in the lab, and we expect that any down-regulation of metabolic rate would have been the same for fish exposed to the various temperature treatments. Also, the holding temperature of 16 °C was very similar to the average water temperature at Santa Catalina Island (Padilla-Gamino and Carpenter, 2007). If there were an overall acclimation to temperature conditions in the lab, it would be similar to temperature levels that this population experiences naturally.

Regardless of the mechanisms leading to high thermal sensitivity of *L. dalli*, it is clear that changes in temperature can be a strong driver of changes in metabolism and energetic demand. At higher temperatures

fish may increase consumption to compensate for the costs of metabolism, or they may suffer the consequences of reduced growth, performance, and/or reproduction (Arnott et al., 2006; Brown et al., 2006; Burel et al., 1996). To meet energetic demands at high temperatures, gobies would have to consume prey at an elevated rate. Individual gobies tend to reside on the seafloor near shelters within their home range, and when foraging, they make brief forays away from the shelter and into the water column (Hartney, 1989). Increased consumption would require more time away from the shelter and would incur a greater risk of predation. However, Steele (1998) found that when *L. dalli* were exposed to greater abundances of predators, individuals decreased their foraging rates and hid in shelters for longer periods of time. As a consequence, they exhibited decreased growth rates. It is likely that that there are limits on how much gobies can increase their foraging activities while still remaining safe from predators. When faced with an increase in temperature, *L. dalli* individuals may not be able to fully meet their energetic demands by increased foraging, and may ultimately invest less energy in somatic growth and reproductive output. Larger females have the capacity to produce more eggs, and if energy is limiting at higher temperatures, gobies may produce fewer eggs per female. For *L. dalli* the development of eggs and larvae is accelerated at higher temperatures (Archambeault et al., 2015), and although this may increase survival during early stages, the extent to which these effects would offset the reduction in number of eggs per mother is not clear. This species also has energy demands associated with sex change, and reproductive success is largely determined by functional sex. This is based on a hierarchical ranking system in which a single male is dominant (Rodgers et al., 2005; St. Mary, 1993). When the dominant male is removed, the most dominant female will rapidly increase body size to replace him, and if energetic demands are too high for investment in growth there is potential for females to remain smaller and stay female, thus reducing the ratio of males to females within social groups.

Another trade-off that may occur with increased metabolic demands is the ability to maintain a competent immune system. It has been thoroughly demonstrated that any type of up-regulation in an immune response is metabolically costly for the host and can increase the risk of infection (see review by Lochmiller and Deerenberg, 2000). Increasing temperature can alter immune function, and when species are near their thermal maxima both innate and acquired immune functions tend to be suppressed (Dittmar et al., 2014). This phenomenon has been demonstrated for three-spine sticklebacks that were exposed to a simulated heat wave and subsequently exhibited long lasting immune disorders and higher mortality rates (Dittmar et al., 2014). Throughout the summer months of the 2015 El Niño event there were numerous *L. dalli* individuals showing signs of disease (i.e., fungal infections, fin rot, etc.) and high mortality rates were observed in the field at Catalina Island and within the laboratory (R. Rangel, *personal observation*). During this time in 2015, average sea surface temperatures in the Southern California Current System were sustained at levels of 3–5 °C above average until approximately July 2016 (Gentemann et al., 2017; Zaba and Rudnick, 2016). These observations, combined with our laboratory studies of metabolism suggest that having a high thermal sensitivity may cause a trade-off between metabolism and immune system defense for *L. dalli*. We suggest that more studies of this species' physiology and responses to temperature are needed to help us better estimate how or if populations of *L. dalli* will be able to thermally adapt and survive under changing climate conditions and increasing temperatures in the future.

Acknowledgments

We would like to thank Sarah Luongo, Jillian Sawyna, Mark Steele, and Ryan Logan for help with collection of specimens, and Connor White for data analysis assistance. Yvette Ralph, Kiersten Darrow, as well as numerous undergraduates help with husbandry and animal care. We would also like to thank Christopher Lowe and Lisa Mastro for use of lab equipment, as well as Larry Allen for supplying the drawing of *L. dalli*. R. Rangel received support from Southern California Tuna Club, Los Angeles Rod and Reel Club, the Reish Grant for Graduate Research, California State University Long Beach summer research assistantship, and Council on Ocean Affairs, Science and Technology graduate student research award.

Appendix 1. Estimates of Q_{10} for metabolic rates and oxygen consumption of small benthic fishes

Species	Q_{10}	Climate	Habitat	Authors	Year	Journal	Weight (g)	Notes
Clinocottus analis	1.70	Temperate	Intertidal	J. B. Graham	1970	Copeia	12.0	Collected during winter
Clinocottus analis	3.30	Temperate	Intertidal	J. B. Graham	1970	Copeia	12.0	Collected during summer
Hypsoblennius gilberti	2.10	Temperate	Intertidal	J. B. Graham	1970	Copeia	10.0	Collected during winter
Hypsoblennius gilberti	2.60	Temperate	Intertidal	J. B. Graham	1970	Copeia	10.0	Collected during summer
Bathygobius fuscus	1.12	Tropical	Intertidal	J. Eme and W.A. Bennett	2009	Australian Journal of Zoology	0.9	
Bathygobius sp.	1.06	Tropical	Intertidal	J. Eme and W.A. Bennett	2009	Australian Journal of Zoology	0.3	
Abedufduf sordidus	1.26	Tropical	Reef	J. Eme and W.A. Bennett	2009	Australian Journal of Zoology	0.2	
Dascyllus aruanus	2.65	Tropical	Reef	J. Eme and W.A. Bennett	2009	Australian Journal of Zoology	0.4	
Apogon novemfasciatus	2.29	Tropical	Reef	J. Eme and W.A. Bennett	2009	Australian Journal of Zoology	1.1	
Liza vaigiensis	2.03	Tropical	Reef	J. Eme and W.A. Bennett	2009	Australian Journal of Zoology	1.5	
Rypticus nigripinnis	1.94	Tropical	Intertidal	J. B. Graham	1972	Physiological Zoology	5.0	
Bathygobius ramosus	1.83	Tropical	Intertidal	J. B. Graham	1972	Physiological Zoology	5.0	

Apogon dovii	2.74	Tropical	Reef	J. B. Graham	1972	Physiological Zoology	5.0	
Oligocottus snyderi	3.20	Temperate	Intertidal	R. W. Morris	1961	Physiological Zoology	2.0	Collected from Oregon
Oligocottus snyderi	2.80	Temperate	Intertidal	R. W. Morris	1961	Physiological Zoology	2.2	Collected from California
Clinocottus globiceps	3.60	Temperate	Intertidal	R. W. Morris	1961	Physiological Zoology	6.2	
Clinocottus recalvus	2.80	Temperate	Intertidal	R. W. Morris	1961	Physiological Zoology	5.4	
Clinocottus analis	2.90	Temperate	Intertidal	R. W. Morris	1961	Physiological Zoology	5.2	
Oligocottus maculosus	2.10	Temperate	Intertidal	R. W. Morris	1961	Physiological Zoology	6.7	
Acanthochromis polyacanthus	1.50	Tropical	Reef	J. L. Rummer et al.	2014	Global Change Biology	4.4	
Dascyllus melanurus	2.10	Tropical	Reef	J. L. Rummer et al.	2014	Global Change Biology	3.0	
Cheilodipterus quinqielineatus	1.40	Tropical	Reef	J. L. Rummer et al.	2014	Global Change Biology	3.3	
Pomacentrus moluccensis	7.20	Tropical	Reef	J. L. Rummer et al.	2014	Global Change Biology	2.9	
Chromis atripectoralis	4.80	Tropical	Reef	J. L. Rummer et al.	2014	Global Change Biology	2.6	
Zoramia leptacantha	1.70	Tropical	Reef	J. L. Rummer et al.	2014	Global Change Biology	1.0	
Gobius cobitis	2.30	Temperate	Intertidal	P. Berschick et al.	1987	Journal of Experimental Biology	60.0	
Gillichthys mirabilis	3.97	Temperate	Intertidal	G. W. Barlow	1961	The Biological Bulletin	1.0	Collected from San Francisco
Gillichthys mirabilis	2.84	Temperate	Intertidal	G. W. Barlow	1961	The Biological Bulletin	1.0	Collected from San Felipe
Gillichthys seta	2.01	Temperate	Intertidal	G. W. Barlow	1961	The Biological Bulletin	1.0	Collected from Puertecitos
Gillichthys mirabilis	5.17	Temperate	Intertidal	G. W. Barlow	1961	The Biological Bulletin	1.0	Collected from Salton Sea
Sebastiscus marmoratus	4.69	Temperate	Reef	J. Kita et al.	1996	Marine Biology	13.0	
Caffrogobius caffer	1.82	Temperate	Intertidal	J.O.G. Kemp	2009	African Zoology	8.4	
Diplodus sargus capensis	2.07	Temperate	Intertidal	J.O.G. Kemp	2009	African Zoology	0.5	
Lythrypnus dalli	5.21	Temperate	Reef	R. Rangel and D. W. Johnson		This study	0.83	

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